

Modeling the disappearance of the Neanderthals using principles of population dynamics and ecology



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ABSTRACT

Current hypotheses regarding the disappearance of Neanderthals (NEA) in Europe fall into two main categories: climate change, and competition. Here we review current research and existing mathematical models that deal with this question, and we propose an approach that incorporates and permits the investigation of the current hypotheses. We have developed a set of differential equations that model population dynamics of anatomically modern humans (AMH) and NEA, their ecological relations to prey species, and their mutual interactions. The model allows investigators to explore each of the two main categories or combinations of both, as well as various forms of competition and/or interference within the context of competition.

The model is designed to include a wide variety of hypotheses and associated archaeological evidence, not focused on a particular hypothesis regarding NEA extinction. It therefore provides investigators with a model to impartially examine various hypotheses (individually or in combination) regarding climatic effects, differential resource use, differences in birth/death rates and carrying capacities, competition, interference, disease, interbreeding, and cultural distinctions that might have led to the extinction of NEA. Moreover, the model accommodates the design of scenarios concerning—for example—population growth, hunting, competitive interactions, cultural differences, and climatic influences to investigate which concepts best explain the rapid disappearance of NEA.

In addition, our model is a modification of the classical Lotka-Volterra model for a wide range of any two populations competing for a common resource. Specifically, our model explicitly includes the resource as an additional variable, a dependence of important population parameters on resource, as well as accommodates treating one of the populations as invasive.

1. Introduction

Neanderthals (NEA) originated approximately 400,000 years ago and lived in Europe and western Eurasia through at least two cycles of glacial and interglacial conditions (Stringer et al., 2003). Neanderthal geographical distribution, as well as mitochondrial DNA comparisons with anatomically modern humans (AMH), suggest that the two lineages share a common ancestor between 270,000 and 440,000 years ago (Green et al., 2010). In palaeoanthropology, species are differentiated by morphology (Mayr, 1965; Fox, 1986) rather than by potential for interbreeding. It is thus difficult to know on the basis of appearance alone whether NEA and AMH were the same species. Anatomical studies have led NEA and AMH to be described as either close sister species (Delson and Harvati, 2006) or as subspecies (Smith et al., 2005; Trinkaus, 2007), and genetic evidence suggests several

periods in the past that AMH and NEA may have interbred to a certain extent (Kuhlwilm et al., 2016; Prüfer et al., 2014). In any case, the two hominids appear to have had similar ecological requirements and a large degree of overlap in resource use, including predation on large herbivores such as reindeer—*Rangifer tarandus* (Grayson and Delpech, 2008; Richards and Trinkaus, 2009).

NEA were the only hominids living in Europe until about 44,000 years ago (Verna et al., 2012), when AMH arrived. NEA appeared to be well adapted to a range of climatic zones, and may have inhabited both woodland and tundra steppe regions (Gaudzinski-Windheuser and Roebroeks, 2011). Recent research (Banks et al., 2008; Higham et al., 2014) indicates the last NEA sites date to no later than 39,000 years ago. NEA disappearance from their extensive range thus occurred within 5,000 years of the arrival of AMH in the regions occupied by NEA.

The time period of primary concern in this paper is the relatively

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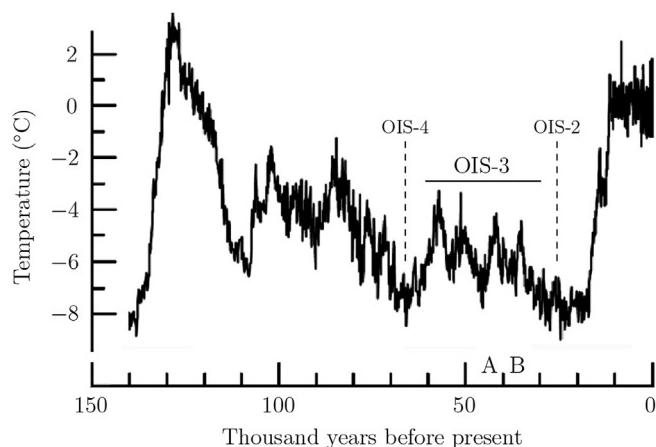


Fig. 1. Temperature (compared to today) over the last 150,000 years, based on ^{18}O and ^{16}O ratios from Antarctic ice cores. Most of the record is the last glacial period, but the previous interglacial is shown as well. Relative cool periods (OIS-2 and OIS-4) flank the warmer OIS-3, which lasted from 60,000 to 27,000 years ago. AMH arrived in Europe at A (about 44,000 years ago). The NEA disappeared from Europe at B (39,000 years ago), before cool climates returned at the end of OIS-3. Temperature data from Petrie et al. (1999).

warm interstadial called Stage 3 (OIS-3, or Oxygen Isotope Stage 3; Fig. 1) between 60,000 and 27,000 years ago (van Meerbeeck et al., 2009). Stage 3 was preceded by the cold OIS-4 and followed by the even colder OIS-2—also called the Late Glacial Maximum, or LGM (24,000 to 19,000 years ago, van Meerbeeck et al., 2009).

Studies relating to NEA disappearance are of two types: archaeological and mathematical. As a rule, the archaeological studies focus on evidence from sites providing skeletal remains and tool technologies while mathematical studies use approaches based on ecological population models. Whatever the type of study, explanations for NEA disappearance fall into two major groups. The first focuses on climatic influences that might have directly influenced survival or have led to loss of food resources (Finlayson, 2004). The second deemphasizes the importance of climate and focuses on interactions between NEA and AMH that might have led to the replacement of NEA (Banks et al., 2008; Gilpin et al., 2016; Mellars, 2004; Zubrow, 1989, 2000), which includes interbreeding followed by absorption (Smith et al., 2005).

For the most part, those studies based on mathematical models have been theoretical, with minimal use of archaeological data; in turn, mathematical modelers have generally not accounted for specific archaeological findings. Archaeologists have not always embraced—or even mentioned—mathematical modeling studies. An exception is Stringer et al. (2003), who described the implications of most of the NEA extinction mathematical models then available. Our intention is to enhance communication between these two sets of researchers by illustrating ways in which integration of an appropriate mathematical model with archaeological data can help test the various hypotheses regarding the fate of the NEA.

We will first briefly review the archaeological studies, focusing on the claims of proponents of *climatic* versus those of *competition* hypotheses. We will next examine various mathematical modeling approaches that have been used, and finally we will propose a model of our own that uses concepts of population dynamics and ecology.

Our model is inclusive of a wide variety of hypotheses and therefore should allow testing of any hypothesis (individually or in combination) for the mechanism of NEA extinction. We do not focus on whether climate, competitive interactions, or any other ecological or cultural feature caused NEA extinction. Instead, the paper is intended to provide an accessible and inclusive platform by which investigators might test their own hypotheses regarding the population dynamics of NEA and AMH, as well as to identify the relevant parameters that need

estimating based on archaeological evidence. Moreover, the model is designed to accommodate numerous parameters, whose values correspond to archaeological data that reflect—for example—the population ecology, competitive interactions, interference, disease, interbreeding, or cultural differences between the two populations.

In addition, while we frame our model in terms of the two populations NEA and AMH, it is a modification of the classical Lotka-Volterra model for any two populations competing for a common resource. Specifically, our model explicitly includes the common resource as an additional variable, a dependence of population parameters on resource, as well as accommodates treating one of the populations as invasive.

2. Current hypotheses for NEA extinction

In this section, we discuss the current hypotheses regarding *when* NEA became extinct, as well as *why* they became extinct. The hypotheses for NEA extinction fall into two main categories: climatic adaptability of NEA or competition. We identify several topics of current discussion that influence how one approaches modeling the population dynamics of NEA and AMH: specifically, the discussions over (1) the dates of latest NEA remains, (2) the level to which NEA were cold-adapted, (3) the degree of overlap in resource use, and (4) the various types of interference between NEA and AMH.

2.1. Dates of latest NEA remains

Much of the current discussion is affected by the accuracy with which the timing of NEA disappearance is known. NEA sites in Iberia were originally reported to have later dates for the last NEA occupation levels than did sites farther north. Hypotheses (e.g., Finlayson, 2004) that climatic change affects NEA disappearance depend on these late dates (approximately 24,000 years ago) for NEA sites in Iberia. By then, the LGM had arrived in northern Europe and if NEA were forest-adapted, they would need to move south. In addition, such movement would reduce the probability of competition with AMH.

However, Wood et al. (2013) reevaluated the late ^{14}C dates from 11 sites in Iberia, concluding that dates from nine of these sites were based on inappropriate carbon samples and are not trustworthy. Materials from the two datable sites gave dates more than 10,000 years older than earlier estimates. Together these data suggest that there is no reliable evidence that NEA were present in southern Iberia more recently than 42,000 years ago. This conclusion is consistent with another new study (Higham et al., 2014) that indicates that nowhere in Europe are there reliably dated NEA sites younger than 39,000 years ago.

Any model that attempts to propose a cause for NEA extinction must accommodate the archaeological evidence indicating that NEA in Europe were gone by approximately 5,000 years after AMH arrived. In this paper we provide four simulations of our model that achieve this result as required (see Section 5.3). Another value of the simulations is that each is based on a different hypothesis for NEA extinction, illustrating the inclusive nature and flexibility of our model. This approach of beginning with an inclusive model that does not focus on one specific hypothesis allows investigators to broadly adapt mathematical (theoretical) models with archaeological discoveries (perhaps including discoveries yet to occur) and data with impartiality.

2.2. Climatic adaptability of NEA

The NEA disappeared before the end of OIS-3 (B in Fig. 1). They flourished during both cooler and warmer climates prior to the arrival of AMH, who arrived about 44,000 years ago (A in Fig. 1). Even so, it is a matter of discussion whether NEA's disappearance is better explained by climatic change or by competition with AMH.

NEA adaptations to the climatic conditions of Pleistocene Europe have been studied for decades (Beals et al., 1984; Trinkaus, 1981). NEA

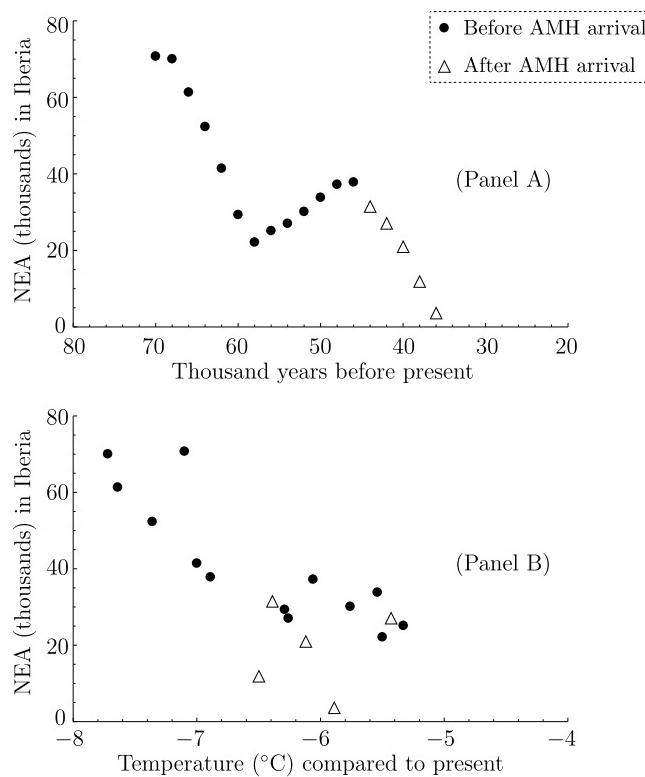


Fig. 2. Neanderthal populations in Iberia in relation to time and temperature. In both panels, closed symbols represent NEA populations before arrival of AMH in Europe at about 44,000 years ago, while open symbols represent NEA populations after arrival. Panel A: Numbers of NEA in Iberia taken from Figure 7.16 in Finlayson (2004). Panel B: Plot of NEA populations in Iberia versus temperature as obtained from the oxygen isotope values (Petit et al., 1999) shown in Fig. 1.

were present in central and western Europe at a time of greater cold than today, and proportions of limb bones (Aiello and Wheeler, 2003; Trinkaus, 1981) and brain volume (Beals et al., 1984) are consistent with their being at least as cold-adapted as modern humans who now inhabit the most northern latitudes.

Because this issue can be important in the question of NEA extinction, we developed a graphical method to determine the relative importance of climatic influences and competitive interactions between NEA and AMH. We attempted this by combining estimations of NEA numbers in Europe, based on the model of Finlayson (2004), between 70,000 and 38,000 years ago with the oxygen isotope-derived temperature estimates for the same time period (see Fig. 2).

Any analysis of this sort is hampered by the difficulty of assigning dates to late NEA sites; we used the simulation of Finlayson (2004) because in his model for NEA in Iberia, NEA disappeared about 38,000 years ago (see Fig. 2A). If Finlayson's estimates for NEA population changes are realistic, then combining his model with the oxygen isotope record (Petit et al., 1999) (see Fig. 2B) suggests that NEA had a wide temperature tolerance and that their abundance did not decrease in times of relative cold. However, following the arrival of AMH, numbers of NEA declined rapidly despite moderate temperatures and they disappeared well before the LGM in Europe.

These data (Finlayson, 2004) are not the only NEA population numbers that can be used to study NEA temperature relationships, and we suggest that other researchers may want to make additional correlations between climate and the NEA–AMH overlap. We present them only to propose that it is possible to use graphical approaches to separate the question of NEA climatic tolerance from the possible effects of competition/interference between NEA and AMH.

2.3. Competition and interference

Competition is often (e.g. Hardin, 1960) described as an “exclusion” process, in which only one of two closely related populations can survive in a region. The principle is usually taken to refer to separate species, but Hardin was not so restrictive: he merely required that the principle govern two “non-interbreeding populations” occupying “the same niche” in “the same geographic territory.” If one of the two populations has a higher population growth rate, that population will replace the other. Our proposed model can incorporate all these ideas: first, it does not require that NEA and AMH are different species, only that the level of interbreeding is low; second, it is consistent with archaeological data showing that the two populations occupied the same geographical area during OIS-3; third, it is consistent with archaeological data showing that sufficient overlap in resource use was present; fourth, the birth and death rates of NEA and AMH can be set by investigators. The model can thus accommodate the various situations, including scenarios involving several components of interference and/or competition (see Sections 2.3.1 and 2.3.2). The model is not constructed to focus on a particular hypothesis regarding NEA extinction; rather, the model is designed to be inclusive of a wide variety of hypotheses and associated archaeological evidence and data. The inclusiveness of the model provides investigators with an accessible resource to examine various hypotheses (individually or in combination) with impartiality.

2.3.1. Competition between NEA and AMH

Opinions differ as to the degree of dietary similarities between NEA and AMH. Grayson and Delpech (2008) analyzed remains from a site in France containing both late NEA and early AMH remains; they suggested that the diets of the two groups had extensive overlap. Drucker and Bocherens (2004) and Richards and Trinkaus (2009) came to a similar conclusion using nitrogen and carbon stable isotope signatures from NEA and AMH bone collagen. All of these studies suggest that both NEA and AMH were among the top carnivores during the last glacial episode. Both groups hunted and ate large herbivores, and the primary difference between them was a greater reliance on fish among the AMH (Richards and Trinkaus, 2009).

In contrast, Finlayson et al. (2000) and Stewart (2004), argue that prey species found in NEA sites are more likely to be characteristic of forest habitat as compared to species found in AMH sites, thus suggesting a geographic separation and a more limited competition between the two.

2.3.2. Interference between NEA and AMH

Another interaction between human populations that can lead to competition, is termed *interference*: one group may interfere with another—resulting in a competitive advantage for one group by limiting access to resources or living sites, or via interactions that affect birth rate, death rate, carrying capacity, hunting efficiency, etc. Here we briefly mention the current way of describing interference between the two populations. Our model is designed to be inclusive of all potential types of interference and any associated archaeological discoveries, providing investigators with a model to examine various hypotheses (individually or in combination) with impartiality (see Section 5).

Difference in culture levels. A difference in culture levels or learning ability could lead to a competitive advantage for one of the populations. Indeed, Aiello and Wheeler (2003) suggest that NEA were physiologically slightly better cold-adapted than AMH; any advantage that AMH might have had in cold weather probably resulted from cultural adaptations. Cultural differences might also involve more efficient tools, more climate-appropriate clothing (Collard et al., 2016), or division of labor within the AMH population (Horan et al., 2005), as well as better economic organization such as wider trading alliances (Gilpin et al., 2016; Horan et al., 2005).

Physiological differences. A physiological difference between the two

populations could lead to a competitive advantage for one of the populations. Some examples of physiological differences might include: higher birth rates and/or lower death rates for any level of resource, efficiency of resource use and predation, disease resistance, and wider climatic tolerances.

Epidemics. One population could pass a disease to the other. The host population might not be significantly affected because it might already have developed a tolerance to the disease, but the population encountering the new disease might suffer significantly (Houldcroft and Underdown, 2016).

Conflict. Warring populations could result in one population dominating the landscape. This might occur if conflict directly reduces numbers or reduces access to resources.

Interbreeding. Genetic evidence suggests that NEA and AMH did interbreed to a limited extent (Green et al., 2010; Kuhlwilm et al., 2016; Prüfer et al., 2014; Smith et al., 2005). The effects of interbreeding on the relative population dynamics of NEA and AMH could be investigated by assuming that any hybrid offspring live with one of the populations (for example, the mother's group) and do not form a separate population.

3. Mathematical modeling of population dynamics

Much progress has been made in field studies of the dynamics of animal and human populations (Hutchinson, 1978), and researchers recognize that mathematics is helpful to bridge the gap between experimental observations of individual populations and an understanding of the large-scale features of interacting populations in space and time (Murray, 2003). The goal of such modeling is not to account for all processes; rather, it is to understand the major interactions and to develop ways of predicting interactions that may occur under other environmental conditions. Moreover, a model that is flexible (not simply replicating a specific scenario or dataset) allows an investigator to compare the relative importance of various effects (environmental, ecological) on the population dynamics within an accessible platform.

Archaeological and mathematical hypotheses often are thought to be different ways of studying populations; however, both are equivalent models of reality in the sense that the conclusions derived from each depend on interpretation of data. In the case of archaeological models, lithic or fossil data may be limiting; in the case of mathematical models, knowledge of population parameters may be limiting. Both methods should come to the same conclusions if they include comparable and relevant data. Thus, if models are designed around a tractable biological problem and use sound ecological principles, the results should permit predictions that are scientifically interesting and quantifiable (Murray, 2003). In Section 5 we propose such a model, as well as provide four simulations (see Section 5.3) that illustrate the usefulness of incorporating mathematical models with archaeological evidence.

Population models often employ measures of growth rate, carrying capacity, competitive interactions, and climate interactions. They can be simple or complex, but if generality, inclusiveness, and applicability are the goals, then they should be formulated in such a way as to apply to a wide range of populations (like the classical logistic equation and Lotka-Volterra model), to yield mathematical results that are relevant and consistent with archaeological discoveries, as well as to provide a setting to test various realistic hypotheses. For example, there are valid reasons to incorporate the following into a mathematical model of population dynamics:

- Birth and death rates are controlled by different biological factors; we propose it is important to model them separately rather than combining them into a single expression called "growth rate." For example, birth rate increases with resource and death rate decreases with resource, and the functions relating these dependencies are different (see Section 5.2, and Figs. 3 and 4).
- The carrying capacity (an upper limiting population) of a population

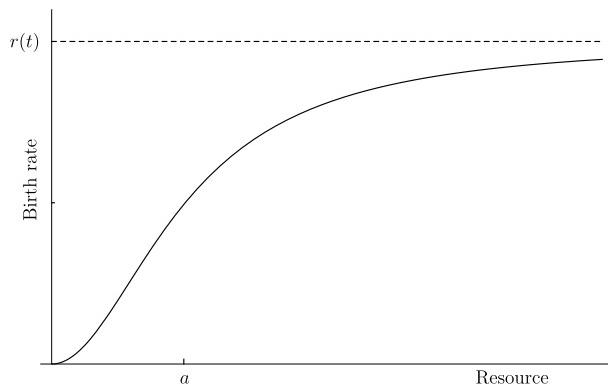


Fig. 3. Relation between population birth rates (either NEA or AMH) and the Resource on which it depends (e.g., reindeer). Birth rate is low at low Resource and increases to its maximum only at high Resource availability. The value a on the horizontal axis is the value of Resource at which birth rate is half maximal. Here a represents either a_1 or a_2 in Equations (1) and (2). The maximal birth rate $r(t)$ can be either a constant or a function of environmental temperature. Here $r(t)$ represents either $r_1(t)$ or $r_2(t)$ in Equations (1) and (2).

is typically treated as a constant (Hutchinson, 1978; Murray, 2003). We allow for the possibility that carrying capacity varies with resource (see Section 5.2 and Fig. 5).

- Hunting success can be estimated by using ecological equations of resource use (functional response models) that estimate predator hunting efficiency. Three distinct models have been developed, each representing a different level of hunting efficiency (Murray, 2003). We are using the most general type of functional response in our model (see Equation (3) and Fig. 6).
- Interactions between human populations are of two types: direct interference of one group on another, and competition for resources (Hutchinson, 1978; Murray, 2003). The two are independent of each other and we have modeled them separately. Interference is modeled with a term that is proportional to the products of the two population sizes (Kot, 2001). (We model interference by the expressions of the form kxy in Equations (1) and (2).) Competition for Resource is modeled by expressions that reduce Resource numbers as NEA and AMH populations rise. (We model competitive interaction by the final two expressions in Equation (3)).
- The increase in population of AMH in western Europe after 44,000 years ago came from two separate factors: continued immigration from eastern Europe, and births to the AMH already resident in western Europe. Models can use both inputs to predict population growth (We model immigration by the final term in Equation (2).).

An effective mathematical model provides a theoretical framework for realistic simulations of population dynamics that are inclusive of current hypotheses, adaptable to new hypotheses or discoveries, as well as offering archaeologists a framework for which population parameters need to be estimated; thus, providing guidance on which attributes to focus on when gathering and evaluating data based on archaeological evidence.

To our knowledge, our proposed model (see Section 5) is the first published model that explicitly addresses the above characteristics.

4. Hypotheses and previous mathematical models

Previous models have been constructed to demonstrate the operation of either the *climatic hypothesis* (Finlayson, 2004; Finlayson et al., 2000) or the *competition hypothesis* (Faria, 2000; Flores, 1998; Sørensen, 2011; Zubrow, 1989, 2000; Gilpin et al., 2016). It appears that none of these models are designed to allow the alternative hypothesis (either climatic or competition) to be tested within its own structure. Further, not all authors present equations that can be

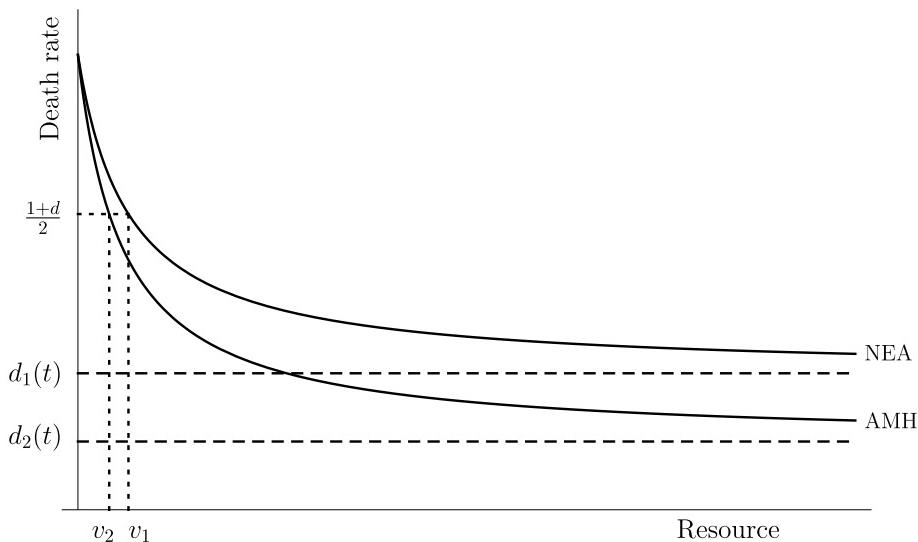


Fig. 4. Relation between population death rate and the Resource on which it depends. Death rate is maximal at zero Resource, and declines to a minimum value as Resource becomes more abundant. The minimal death rates can be either a constant or a function of environmental temperature; $d_1(t)$ and $d_2(t)$ are the minimal death rates for NEA and AMH, respectively in Equations (1) and (2). The parameters v_1 and v_2 are the value of Resource at which death rate is half maximal. In this example, both $d_1(t)$ and v_1 are greater than $d_2(t)$ and v_2 , so NEA have higher death rates at any value of Resource than do AMH.

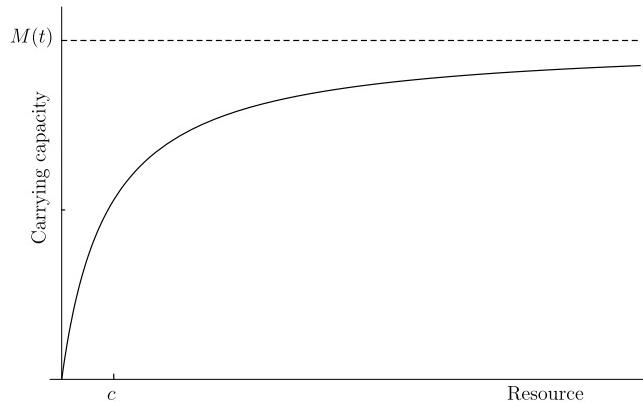


Fig. 5. Relation between carrying capacity (either AMH or NEA) and the Resource on which it depends. The maximal carrying capacity $M(t)$ can be either a constant or a function of environmental temperature. Here $M(t)$ represents either $M_1(t)$ or $M_2(t)$ in Equations (1) and (2). The parameter c is the value of R at which carrying capacity is half maximal. Here c represents either c_1 or c_2 in Equations (1) and (2).

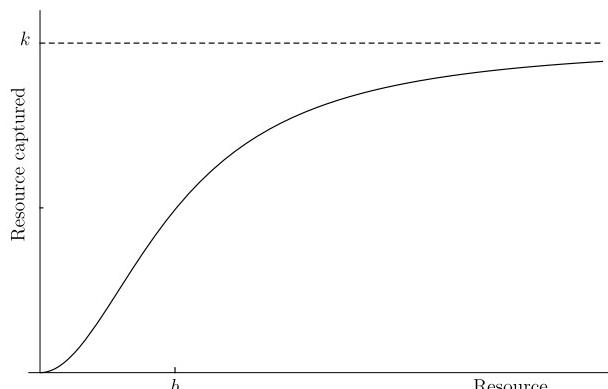


Fig. 6. Relation between Resource and the rate of capture by predators (NEA and AMH). In this functional response curve, the parameter k is the maximal capture rate, and b is the value of R at which the rate of capture is half its theoretical maximum. The parameter k is either k_3 or k_4 , and b is either b_1 or b_2 in Equation (3).

evaluated by others; of those with a recognizable mathematical format, some are based on solutions to difference equations and others are based on solutions to differential equations. We will describe the models within the context of the hypothesis (either climatic or competition) they are investigating.

4.1. Climate/geography

The climatic/geographical model of NEA extinction hypothesizes that NEA were primarily woodland dwellers rather than plains dwellers, and pursued a varied meat/vegetable diet. They evolved in Eurasia during a period of relative warmth and forest dominance; their survival in the northern latitudes was therefore limited to areas in which local climates could maintain open forest habitats and the herbivore species that inhabit them (Finlayson et al., 2000).

Finlayson (2004; Finlayson et al., 2000) has developed a density-dependent population dynamic model taking climate and geography into account. It breaks Iberia up into 273 squares of size 50×50 km; each square has a geographic description, and is assigned one of several climatic conditions depending on time during the glacial period. The model allows movement of NEA or AMH populations from one square to an adjacent one according to geographic and climatic conditions in that square. Neanderthals are modeled as a warm-adapted woodland group; AMH are modeled as a cold-adapted plains group.

Finlayson proposes two features that are testable experimentally; first, that NEA were not cold-adapted, but were hunters of the temperate woodlands who were forced to move southward to follow game during cold episodes. He hypothesizes that moderate climates in OIS-3 allowed NEA to move north; then as the LGM of OIS-2 caused the return of colder temperatures, the deciduous woodland zone of Iberia moved to North Africa. Unlike the forests, the NEA could not cross the Mediterranean Sea, and their forage disappeared from Europe, reducing their ability to maintain populations.

Second, Finlayson proposes that at this time, AMH were not present in Iberia; hence, the demise of the NEA cannot be associated with competitive interactions. Thus, he does not include the competition hypothesis in his model.

4.2. Competition/absorption

Flores (1998) was the first to use a modified logistic equation in the

form of a system of nonlinear ordinary differential equations (ODEs). Specifically, he considers a competitive model where NEA and AMH have a common birth rate and demonstrates that a slightly higher death rate for the NEA is sufficient to explain the extinction of NEA in 5,000–10,000 years after the arrival of AMH.

Faria (2000) considers a system of three nonlinear ODEs to describe how resources, NEA and AMH interact. He examines four hypotheses for NEA extinction—competition, genocide, disease, and interbreeding—and concludes that none of them is sufficient to explain NEA extinction. Faria claims that coexistence is possible under his model, but it is not clear whether the relationship between the various parameters that allow coexistence is based on archaeological data, or if the relationship is merely a consequence of the structure within the three ODEs. In addition, it is not clear whether one can use Faria's model to predict a range of likely scenarios for population change in the NEA and AMH.

Zubrow (1989) models possible scenarios for the interaction between NEA and AMH. The model includes four major groups of parameters: initial population sizes, initial growth rates, competition or replacement rates, and the probability that the two populations come into contact. Interactions are modeled with the NEA always being disadvantaged by contact with AMH. He does not reveal the equations used in the model, but his description implies that they are a system of difference equations. Zubrow ran over 300 trials of the model using ranges of values for the parameters and concluded that there is a small set of values that allows the two species to coexist for a reasonable number of generations. In general, predicted NEA extinction almost always occurs between 2,500 and 7,500 years after contact of the two populations. He also concluded that NEA extinction occurred because of small population size in a competitive situation rather than from a lack of adaptive characteristics.

Zubrow (2000) developed a second interactive demographic model for NEA and AMH populations; parameters include age structure, relative fertility, and population mortality rates. Like his earlier model, this one likely consists of difference equations. After multiple trials, he concludes that direct interactions with AMH and a slightly higher mortality of NEA (about 2% higher than that of AMH) predict extinction of NEA between 1,000 and 7,500 years after contact with AMH.

Sørensen (2011) has developed a demographic model in the form of a first-order difference equation, with time step equal to one year, to express the population change of NEA in terms of birth and death rates. He considers several death rate components, including food shortage and climate change. He concludes that both food shortage and climate change are insufficient to explain the extinction of NEA and conjectures that a probable cause was an infectious disease transmitted by the incoming AMH.

Gilpin et al. (2016) have developed a competition model using nonlinear ODEs based on the Lotka-Volterra model that incorporates an index of culture level (e.g., toolkit size, toolkit sophistication, clothing, economic organization, etc.) of a population as a variable interacting with its population size. In particular, each population's carrying capacity is assumed to be an increasing step function of its culture level. The authors investigate the theoretical conditions under which a difference in culture level might result in the competitive exclusion of a relatively large local NEA population by an initially smaller AMH population (ignoring constant immigration by AMH). The authors propose that NEA extinction is more likely to occur when population growth occurs on a shorter time scale than cultural change, or if AMH have much greater learning ability than NEA, or when the competition coefficients of their model depend on differences in culture levels of the species—with AMH having a competitive advantage over NEA.

Most of the above competition models predict NEA extinction within the currently accepted time frame. However, because each model appears to focus on a particular non-climatic hypothesis for NEA extinction, it is not clear how generally applicable the models are to investigating alternative hypotheses other than each one's focus.

5. Model for population dynamics of NEA and AMH

The previous discussion suggests that investigators disagree concerning the question of NEA resource use, their physiological adaptation to and tolerance for different climates of the late Pleistocene, and interactions with AMH. However, we suspect that a model can be constructed to allow tests of all quantifiable hypotheses. In the spirit of stimulating research in this area, we propose a mathematical approach that does not focus on a particular hypothesis, but allows several hypotheses (with each classified as either a climatic or competition hypothesis) to be examined and the roles of each to be tested.

Population models can never completely describe the dynamics of the populations they are modeling. Two important reasons are these: first, any model attempts to describe biological or cultural processes with mathematical expressions that are only approximations of reality; second, the numbers of parameters included in the model are likely to be fewer than the number that are optimal to describe a complex system (Burnham and Anderson, 2002).

With respect to modeling human population dynamics, we chose to include features that cover the primary processes involved, and are able to be quantified in straightforward terms.

Our model is based on the logistic equation of Verhulst with modifications by Lotka and Volterra, allowing terms for competition to be added (Hutchinson, 1978; Murray, 2003). Even so, we view competition in a slightly larger sense than classical models do (similar to the references in Section 4.2), and our model allows investigators to model the effects of differential resource use as an example of competition. We have also included terms to incorporate cultural advantages that might apply to one of the populations, as well as terms modeling the effects of environmental temperature and Resource on important population parameters. Because of this structure, our model does not focus on a particular hypothesis regarding NEA extinction. Instead, it is designed to be inclusive of a wide variety of hypotheses and associated archaeological evidence, therefore providing ways to examine various hypotheses (individually or in combination) with impartiality. In addition, our model is flexible—not simply replicating a specific scenario or dataset, which allow investigators (mathematical modelers and archaeologists) to compare the relative importance of various effects (environmental, ecological) on the population dynamics within an accessible platform. This model is, to our knowledge, the first published model to accommodate predictions of the contributions of population ecology, climate, competitive interactions, interference, disease, interbreeding, and cultural differences between these two populations.

5.1. Mathematical basis for the model

We adopt the *Convention of Continuity* (Hutchinson, 1978), the idea that although real populations consist of discrete individuals, their dynamics can be modeled as if they are continuously varying as long as one is “dealing with a sufficiently large population of organisms not having definite breeding, or dying, seasons, in which reproduction occurs at random among all members of the appropriate age class, and death occurs according to some statistically defined pattern not varying with time.” This convention allows for the use of differential equations and their solution by calculus (Hutchinson, 1978). The alternative to adopting this convention is to use discrete difference equations, as did Sørensen (2011) and Zubrow (1989, 2000).

As in the references mentioned in Section 4.2, we adopt the position that competition can occur between two closely related populations (whether they are the same species or not) living in the same region and using a common resource (Hardin, 1960).

Recall that the Lotka-Volterra model is the classical model for any two populations that compete for the same resource. It is a system of two nonlinear ODEs with variables for the two populations, but no variable for the common resource that the two populations compete over (Hutchinson, 1978; Murray, 2003). The level of resource (amount

of food) could influence the values of parameters in the Lotka-Volterra model, yet the parameters are treated as constants. For example, more resource (food) may lead to an increase in a population's growth rate and carrying capacity, while less resource (food) may result in a decrease of a population's growth rate and carrying capacity.

Our model is a modification of the Lotka-Volterra model. Indeed, it is a system of three nonlinear ODEs, with variables for the two populations, as well as a third variable corresponding to the common resource—making the common resource an explicit component of the model (unlike in the Lotka-Volterra model). In addition, we also include an immigration term, which allows an investigator the option to treat one of the populations as invasive relative to an already established native population. We point out that if we assume the resource is constant (like in the Lotka-Volterra model) and that both populations are native—setting the immigration term to zero (like in the Lotka-Volterra model), then our model reduces to the classical Lotka-Volterra model, which should be the case for any such modification. To our knowledge, our model is the first modification of the Lotka-Volterra model in this manner. We note that other modifications have focused on increasing the number of competing populations to more than two, while continuing to treat the common resource as a constant (Murray, 2003).

5.2. The model equations

We now frame our model in terms of the two populations NEA and AMH, and a common resource for which they compete. We reiterate that our model is general (much like the Lotka-Volterra model) in the sense that it could apply to a wide range of any two populations competing for a common resource.

We have developed a system of nonlinear ODEs (see Equations (1)–(3)) that predict numbers over time of three different populations: NEA (variable x in Equations (1)–(3)), AMH (variable y in Equations (1)–(3)) and a common Resource (variable R in Equations (1)–(3)), such as reindeer. The three populations have their own birth/death rates and carrying capacities, which can be related to climatic conditions if desired; for example, $r_1(t)$, $d_1(t)$, and $M_1(t)$ in Equation (1) link these items for NEA to temperature changes that occurred in OIS-3 (see the below paragraph discussing climatic influence). The equations also link the growth of the two human populations both to Resource numbers and to possible interactions between them (see Section 2).

Our model assumes that R is used by both AMH and NEA, a situation consistent with archaeological evidence (Grayson and Delpach, 2008; Richards and Trinkaus, 2009).

We discuss the key features of our model below. The equations in our model are solved numerically using the software program Mathematica (Wolfram Research, 2012). The specific details of analyzing the model are presented in a Mathematica Notebook, which is available online as Supplemental Data. This supplement also includes the Mathematica code for the various simulations we include in this paper (see Section 5.3).

Our model consists of the following ODEs:

$$\frac{dx}{dt} = \left(\frac{r_1(t)R^2}{a_1^2 + R^2} - \frac{v_1 + d_1(t)R}{v_1 + R} \right) x \left(1 - \frac{x}{\frac{M_1(t)R}{c_1 + R}} \right) - k_1 x y \quad (1)$$

$$\begin{aligned} \frac{dy}{dt} = & \left(\frac{r_2(t)R^2}{a_2^2 + R^2} - \frac{v_2 + d_2(t)R}{v_2 + R} \right) y \left(1 - \frac{y}{\frac{M_2(t)R}{c_2 + R}} \right) - k_2 x y \\ & + i u \left(1 - \frac{y}{\frac{M_2(t)R}{c_2 + R}} \right) \end{aligned} \quad (2)$$

$$\frac{dR}{dt} = \alpha(t)R \left(1 - \frac{R}{M_3(t)} \right) - \frac{k_3 R^2}{b_1^2 + R^2} x - \frac{k_4 R^2}{b_2^2 + R^2} y \quad (3)$$

where the variables x , y and R correspond to the three populations NEA, AMH and Resource, respectively. The model is purposely designed to be inclusive of a wide variety of hypotheses and associated archaeological evidence; therefore, providing investigators with an accessible model to examine various hypotheses (individually or in combination) with impartiality. Moreover, the model's flexibility (not simply replicating a specific scenario or dataset) provides an investigator an accessible platform to compare the relative importance of various effects (environmental, ecological) on the population dynamics of NEA and AMH.

The following are key features of our model, which we frame in terms of the two populations NEA and AMH. However, like the classical Lotka-Volterra model, our model could be applied to a wide range of any two populations competing for a common resource. To our knowledge, our model is the first published model that includes the following attributes.

Resource dependence. The level of resource (amount of food) could influence the values of the population parameters in the classical Lotka-Volterra model, yet they are treated as constants. For example, more resource (food) may lead to an increase in a population's growth rate and carrying capacity, while less resource (food) may result in a decrease of a population's growth rate and carrying capacity. Our model is a modification of the Lotka-Volterra model in the sense that we do not treat the Resource as a constant; rather, we treat the common resource as its own population that varies with time (see Equation (3)). Thus, we are able to include a Resource dependence on the two competing population's birth/death rates and carrying capacity.

Regarding modeling NEA and AMH population dynamics, we note that the archaeological evidence (Lorenzen et al., 2011) suggests that a significant reduction of resource did not occur during the time period under consideration. Thus, with respect to modeling the two populations NEA and AMH, an investigator may reasonably choose the option to assume that R is a constant in Equations (1)–(3). We reiterate that, in the classical Lotka-Volterra model, an investigator does not have the option of treating the common resource as a variable, and thus is working with a more limited system.

We have chosen to provide a model (a modification of the Lotka-Volterra model) that includes Resource as another variable that varies with time so that our model applies to a wide range of any two populations competing for a common resource—including NEA and AMH, where resource scarcity may (or may not) explicitly occur. The resource scarcity could be due to predation on the resource by the two competing populations and/or by other reasons (e.g., environmental, physiological) related to the resource's growth rate or carrying capacity.

Parameters. When developing a mathematical model, it is important to be mindful of the number of parameters. Decreasing the number of parameters introduces a bias, while increasing the number introduces more variance. See Section 1.4, *Inference and the Principle of Parsimony* in Burnham and Anderson (2002) for a discussion (within a statistical framework) related to issues regarding an optimal number of parameters in a model.

The model is designed to accommodate numerous parameters, whose values correspond to archaeological evidence and data that reflect—for example—the population ecology, competitive interactions, interference, disease, interbreeding, or cultural differences between the two populations.

The three populations NEA, AMH and Resource (x , y and R , respectively) depend on several parameters in Equations (1)–(3), which can be organized into three groups. The parameters:

$\alpha(t)$, $r_1(t)$, $r_2(t)$, $d_1(t)$, $d_2(t)$, $M_1(t)$, $M_2(t)$, and $M_3(t)$

each may accommodate a temperature dependence (or not). The parameters:

a_1 , a_2 , b_1 , b_2 , c_1 , c_2 , v_1 , v_2 , k_1 , k_2 , k_3 , k_4 and i

do not contain a temperature dependence. In addition, the initial population sizes of NEA, AMH and Resource may also be treated as

parameters in the model.

The large number of parameters is a reflection of our model's generality, inclusiveness, and adaptability. Indeed, our model applies to a wide range of populations competing for a common resource (like the Lotka-Volterra model). Our model has the ability to accommodate any of the current hypotheses for NEA extinction, as well as adapt to archaeological evidence and data that reflect—for example—the population ecology, competitive interactions, interference, disease, interbreeding, or cultural differences between the two populations NEA and AMH. In addition to the previous broad discussion of the archaeological merit (see Section 3), please see Section 5, and in particular Section 5.3, for some specific illustrations (via the four simulations) of our model's merit.

Recognizing that a reader may be overwhelmed by the number of parameters (in our model or in any model), we offer some broad suggestions/strategies on how to frame them. First, it may be possible to organize the parameters into natural groupings. For example, as we discuss below, the parameters associated with NEA and AMH may be organized into seven groupings, which seems less daunting than considering each parameter individually: birth rate, death rate, carrying capacity, climatic influence, competition, interference, and the immigration of AMH. Second, an investigator might restrict the number of parameters by considering a null hypothesis; for example, corresponding parameters for NEA and AMH are assumed to have the same value unless there exists archaeological evidence to the contrary. Thus, for example, an investigator might assume the birth rate and carrying capacity parameters are equal ($r_1(t) = r_2(t)$, $a_1 = a_2$, $M_1(t) = M_2(t)$, $c_1 = c_2$), reducing the parameters under consideration by four. Third, an investigator may perform a sensitivity analysis (see Section 5.6) to gain insights into which parameters are the most influential with regard to the population dynamics of NEA and AMH, and focus on running simulations with respect to those parameters.

Birth and death rates. NEA (Equation (1)) and AMH (Equation (2)) populations are each modeled by modified logistic ODEs in which the growth rate = birth rate – death rate.

Our model allows the birth/death rates to vary with Resource, which is a modification of the classical Lotka-Volterra model, where birth/death rates are assumed to be constants.

Birth rate is modeled as an increasing function of Resource availability. Births are less frequent at low Resource, but approach the population's maximal birth rate as food availability increases. Indeed, any expression for birth rate should satisfy the biologically based (boundary) conditions:

- As R increases (more food available), the birth rate will increase.
- Birth rate = 0 when $R = 0$ (no food).
- As $R \rightarrow \infty$ (unlimited food), the birth rate remains bounded and approaches its maximum value.

The expressions

$$\frac{r_1(t)R^2}{a_1^2 + R^2} \quad \text{and} \quad \frac{r_2(t)R^2}{a_2^2 + R^2}$$

satisfy the conditions; moreover, the expressions are the birth rates for NEA and AMH, respectively in Equations (1) and (2). In each expression, the parameter $r(t)$ is the maximal birth rate and a denotes the value of R for which the birth rate is half maximal.

We note that these are not the only expressions that satisfy the desired conditions. We have chosen to model birth rates with this type of functional response curve, which is often referred to as a Type III curve (Murray, 2003), because of its structure at low values for R . Specifically, a population may have difficulty finding and/or killing prey (resource) when prey numbers are low. This difficulty would inhibit a population's ability to "convert" the resource to its birth rate, and the birth rate would experience a corresponding "response lag." Of

all the standard functional response curves, the Type III curve is the one that best models this feature (Murray, 2003). See Fig. 3 for the graph of a birth rate.

There are other factors besides R that influence a population's birth rate; for example, environmental conditions, spatial constraints, physiology, hunting strategies, and culture level. These components can be incorporated via the values of the parameters $r(t)$ and a .

Death rate depends inversely on Resource, unlike birth rate, and so it is appropriate to model it separately from birth rate. The death rate for either human population is high at zero Resource and approaches a minimal positive value at large Resource. The death rate is defined as 100% if there is no Resource. Indeed, any expression for death rate should satisfy the biologically based (boundary) conditions:

- As R increases (more food available), the death rate will decrease.
- Death rate = 1 (100%; that is, everyone dies) when $R = 0$ (no food).
- As $R \rightarrow \infty$ (unlimited food), the death rate remains positive and approaches its minimum value.

The expressions

$$\frac{v_1 + d_1(t)R}{v_1 + R} \quad \text{and} \quad \frac{v_2 + d_2(t)R}{v_2 + R}$$

satisfy the conditions; moreover, the expressions are the death rates for NEA and AMH, respectively in Equations (1) and (2). In each expression, the parameter $d(t)$ is the minimal death rate and v denotes the value of R at which the death rate is half maximal. We note that these are not the only expressions that satisfy the desired conditions, but are the simplest such smooth curves that do. See Fig. 4 for the graph of the death rates.

Similar to a population's birth rate, there are other factors (see above) besides R that influence a population's death rate, and these other factors can be incorporated via values of the parameters $d(t)$ and v .

NEA likely had higher death rates at any value of Resource than did AMH (Pettitt, 2000); differences in death rate for NEA and AMH are modeled by the differences in v_1 and v_2 , as well as $d_1(t)$ and $d_2(t)$.

Carrying capacity. Similar to the birth/death rates, our model allows the carrying capacity to also vary with Resource; thereby modifying the classical Lotka-Volterra model, where the birth/death rates and carrying capacity are assumed to be constant.

Similar to the birth/death rates, the carrying capacity (the theoretical maximum population) for NEA and AMH is a complex function that also depends on Resource. One option for a modeler is to assume that the carrying capacity is constant (as in the classical Lotka-Volterra model); we have taken a more general approach by allowing it to vary with Resource. The carrying capacity is defined as zero if there is no Resource. Indeed, any expression for the carrying capacity should satisfy the ecologically based (boundary) conditions:

- As R increases (more food available), the population's carrying capacity will increase.
- Carrying capacity = 0 when $R = 0$ (no food).
- As $R \rightarrow \infty$ (unlimited food), the carrying capacity remains bounded and approaches its maximum value.

The expressions

$$\frac{M_1(t)R}{c_1 + R} \quad \text{and} \quad \frac{M_2(t)R}{c_2 + R}$$

satisfy the conditions; moreover the expressions are the carrying capacities for NEA and AMH, respectively in Equations (1) and (2). In each expression, the parameter $M(t)$ is the maximal carrying capacity and c denotes the value of R at which the carrying capacity is half maximal. See Fig. 5 for the graph of a carrying capacity.

We note that these are not the only expressions that satisfy the

desired conditions. We have chosen to model the carrying capacity with this type of functional response curve, which is often referred to as a Type II curve, instead of using a Type III curve as done with the birth rate because we conjecture that the carrying capacity will not necessarily experience a “response lag” at low resource like birth rate (Murray, 2003).

Similar to a population's birth/death rates, there are other factors (see above) besides R that influence a population's carrying capacity, and these other factors can be incorporated via values of the parameters $M(t)$ and c .

We mention that there is a basis for modeling carrying capacity separately from the birth/death rates. Indeed, a situation could arise where a population has a sufficiently large supply of Resource (food) and a large carrying capacity, but small growth rate.

As an illustrative example, consider the polar bear. There could be plenty of seals (food) and a large carrying capacity (large potential maximum population), but the polar bears' ability to kill seals might be diminished by environmental influences (e.g., lack of sea ice), thus affecting the polar bears' birth/death rates—causing the growth rate to be essentially zero or negative; resulting in polar bear numbers stagnating below the carrying capacity or going to extinction even though there are plenty of seals.

We are unaware of any archaeological data or biological evidence that supports a similar situation for NEA or AMH to the polar bear, but if such evidence is discovered or hypothesized, our model will be able to accommodate it, allowing an investigator to examine such a hypothesis; again illustrating the benefit of our inclusive and impartially constructed model.

Climatic influence. The model also can accommodate temperature dependent birth/death rates, as well as carrying capacities, for NEA and AMH and R if desired. Specifically, the maximal birth rates $r_1(t)$ and $r_2(t)$, minimal death rates $d_1(t)$ and $d_2(t)$, and maximal carrying capacities $M_1(t)$ and $M_2(t)$ of the NEA and AMH, as well as the growth rate of the Resource $\alpha(t)$ and carrying capacity $M_3(t)$, may be programmed to vary with temperature. (See the Mathematica Notebook available online, where we use a linear fit relationship between the temperature and time values given in Fig. 1, from A to B in OIS-3. An investigator could alter the Mathematica Notebook to use a nonlinear fit relationship if desired.)

Competition via resource. The Resource R is modeled by Equation (3). In the absence of NEA and AMH, the Resource satisfies a modified logistic ODE with its own growth rate $\alpha(t)$ and carrying capacity $M_3(t)$. The modification is the introduction of the competition terms in Equation (3).

NEA and AMH compete for the common Resource, with each population's predation on the Resource reducing the Resource numbers. Any expression for the predation terms should satisfy the ecologically based (boundary) conditions:

- Hunting success (predation on Resource) is an increasing function with respect to R . Moreover, a hunter tends to find prey less efficiently when R is low (a response lag), then approaches a maximal success rate as R increases (when a population has as much R as needed, increasing R does not increase the hunting success in an unbounded linear manner).
- Hunting success = 0 (no predation) when $R = 0$ (no prey).
- As $R \rightarrow \infty$ (unlimited prey), the hunting success remains bounded and approaches its maximum value.

The expressions

$$\frac{k_3 R^2}{b_1^2 + R^2} \quad \text{and} \quad \frac{k_4 R^2}{b_2^2 + R^2}$$

satisfy the conditions; moreover, the expressions correspond to the competition terms described above for NEA and AMH, respectively in

Equation (3). In each expression, the parameter k is the maximal rate of predation and b denotes the value of R at which the predation rate is half maximal (see Fig. 6 for graphs).

We note that these are not the only expressions that satisfy the desired conditions. We have chosen to model the predation rates with this type of functional response curve, which is often referred to as a Type III curve, because it best represents the above conditions—especially the “response lag” at low values of R compared to the other standard functional response curves (Murray, 2003).

NEA and AMH likely had different hunting strategies and successes—perhaps because of differences in culture level, learning ability or physiology—and these can be made part of the model by an investigator via values of the parameters k and b . In addition to variables and parameters affecting hunting efficiency, the model permits hunting activities of the NEA and AMH to reduce the availability of the Resource. The archaeological evidence (Lorenzen et al., 2011) indicates, however, that a reduction in reindeer populations (Resource) did not occur during the time period under consideration. Thus, the coefficients k_3 and k_4 in our simulations (see Section 5.3 and the Mathematica Notebook available online) are chosen to have very small positive values.

To incorporate cultural differences between NEA and AMH in the analysis, an investigator could consider the situation where AMH had a competitive advantage because of culture level or learning ability. This could be included in the model by assuming $b_2 < b_1$ (AMH are more efficient at killing the Resource) and/or $k_4 > k_3$ (AMH have a higher maximal kill rate of the Resource).

We again mention that our model is general in the sense that it could apply to a wide range (expanding on the range encompassed by the Lotka-Volterra model) of any two populations competing for a common resource. Indeed, unlike the Lotka-Volterra model (because it assumes the common resource is constant), our model can accommodate a situation where predation by one (or both) of the populations on the common resource significantly affects the resource population over time, as well as the situation where predation by both populations does not significantly affect the common resource—as the case for NEA and AMH.

Interference. NEA and AMH also may interact, either directly or indirectly, in ways that influence populations sizes. An optional interference term proportional to the population sizes of each group and consistent with the Lotka-Volterra system of equations (Hutchinson, 1978) is included. For example, the expression k_{1xy} in Equation (1) models the effect of interactions (interference between NEA and AMH) on NEA. If the proportionality constant k_1 is set to zero, no interference occurs and Equation (1) reduces to the structure of the logistic equation. This is similar for the expression k_{2xy} in Equation (2).

To incorporate cultural differences between NEA and AMH in the analysis, an investigator could consider the situation where AMH had a competitive advantage because of culture level or learning ability. This could be included in the model by assuming $k_2 < k_1$. This corresponds to the situation Gilpin et al. (2016) considered, in which their competition coefficients corresponding to our k_1 and k_2 are functions of the population's culture level.

Interbreeding. Interbreeding also could be investigated by treating it as a type of interference. For example, assuming that any hybrid offspring live in the mother's group and do not form a separate population, appropriate alterations to k_1 and k_2 could accommodate an investigator's views as to the specific effects of hybridization.

Immigration of AMH. Archaeological data suggest a consistent immigration of AMH into Europe beginning about 44,000 years ago (Verna et al., 2012). We include an additive term $i u(q)$ to account for population growth by immigration of AMH, as well as by births in place. Indeed, Equation (2) contains the expression

$$i u \left(1 - \frac{y}{\frac{M_2(t)R}{c_2 + R}} \right)$$

for immigration of AMH. The yearly immigration, denoted by i , is of course unknown, but a value for i can be set by the investigator (see the Mathematica Notebook available online). The function $u(q)$ denotes the unit step function: $u(q) = 0$ for $q < 0$, and $u(q) = 1$ for $q \geq 0$, where

$$q = 1 - \frac{y}{\frac{M_2(t)R}{c_2 + R}}.$$

The function $u(q)$ is inserted to maintain AMH population at or below its carrying capacity despite their annual immigration.

Similarly, Currat and Excoffier (2004) include an additive constant immigration term (corresponding to i in our model) as part of their model of the range expansion of AMH, and of their competition and potential admixture with NEA. The authors conclude that AMH did not admix with NEA.

While we have framed the immigration term with respect to treating AMH as an invasive population relative to NEA—an established (native) population, we reiterate that our model applies to a wide range of any two populations competing for a common resource with the option of treating one of the populations as invasive. Indeed, the population corresponding to y in Equations (1)–(3) is the invasive population, while the population x in Equations (1)–(3) corresponds to an already established native population. If both populations are native (similar to the situation in the classical Lotka-Volterra model), then an investigator could simply use $i = 0$ in our model.

Summary of the model. In summary, our model is inclusive in the sense that it allows any investigator to consider various mechanisms as possible scenarios for NEA extinction, including climate, competitive advantage (such as culture level, learning ability, or physiology) interbreeding, epidemics, inter-species conflict, and statistical variation. We reiterate that the model is not constructed to focus on a particular hypothesis regarding NEA extinction. Instead, the model is designed to be inclusive of a wide variety of hypotheses and associated archaeological evidence; therefore, providing investigators with a model to examine various hypotheses (individually or in combination) with impartiality. The model is designed to be flexible (not simply replicating a specific scenario or dataset), which allows investigators (mathematical modelers and archaeologists) to compare the relative importance of various effects (environmental, ecological) on the population dynamics of NEA and AMH within an accessible platform. Moreover, the model is designed to accommodate numerous parameters, whose values correspond to archaeological data that reflect—for example—the population ecology, competitive interactions, interference, disease, interbreeding, or cultural differences between the two populations.

We reiterate that, while we have framed our model in terms of the two populations NEA and AMH, the model is general in the sense that it could apply to a wide range of any two populations competing for a common resource. Moreover, our model is a modification of the classical Lotka-Volterra model by including the common resource as another variable, a dependence of important population parameters on resource, as well as by including an immigration term—allowing an investigator to treat one of the populations as invasive.

To our knowledge, our model is the first published model to have the attributes discussed above.

5.3. Model simulations predicting NEA extinction

Any model that attempts to propose a cause for NEA extinction must accommodate the archaeological evidence indicating that NEA in Europe were gone by approximately 5,000 years after AMH arrived. We have chosen four simulations as illustrations of the model; in all, the NEA go extinct 5,000 years after the arrival of AMH in Europe (i.e., 39,000 years ago) as required.

The four simulations demonstrate two important features of the model: first, that the model is inclusive in the sense that it allows a number of different scenarios to be tested; second, that different mechanisms (i.e., choosing different values for particular parameters) can produce the known result (NEA extinction in 5,000 years after AMH arrival).

Our baseline case, which we do not include as one of our simulations, assumes a slightly higher minimum death rate for NEA than AMH (NEA's growth rate remains positive) consistent with archaeological evidence (Pettitt, 2000), as well as no interference ($k_1 = k_2 = 0$). As expected in this situation, NEA, AMH and Resource populations all approach their carrying capacity (see the Supplemental Mathematica Notebook for complete details).

In each of the four simulations, the NEA and AMH have identical population dynamics parameters (baseline case) except for the tested parameter:

- Cooling climate between 44,000 years ago and 39,000 years ago reduces NEA birth rate and carrying capacity; cooling also increases NEA minimal death rate.
- NEA minimal death rate is higher than that of AMH ($d_1 > d_2$) (see Fig. 4).
- NEA death rate remains higher than AMH death rate at any value of R ($v_1 > v_2$) (see Fig. 4).
- Interference between AMH and NEA is more detrimental to NEA ($k_1 > k_2$).

We did not design the model to propose any particular hypothesis as the cause for NEA disappearance, although we do share some insights that we hope are helpful to archaeologists and mathematical modelers. Specifically, the four simulations are not necessarily meant to demonstrate conclusively that temperature, death rate or interference could be held responsible for the cause of NEA extinction—though one or more of these factors may have played a role; instead, the simulations are presented to illustrate the wide applicability of the model, as well as illustrate how an investigator may compare the relative importance of effects (environmental, ecological) on the population dynamics of NEA and AMH within an accessible platform.

Results for these simulations are given in Figs. 7–10. In each, time starts at 44,000 years ago and ends at 39,000 years ago; original NEA population is set at 20,000 and AMH is set at zero. AMH populations are not graphed, but in all cases they rise rapidly and stabilize at the carrying capacity for AMH (50,000). In each case, Resource remains stable at its carrying capacity (200,000 reindeer), in agreement with paleontological data suggesting that the human presence in Europe did not lead to a decline in reindeer populations between 42,000 and 30,000 years ago (Lorenzen et al., 2011). Only NEA population sizes are affected by the choices in parameters for these simulations. We set the NEA population at 20,000, a value that is arbitrary but is nonetheless in the same range as Finlayson (2004) includes in his model. This value is also consistent with the NEA population estimates of Prüfer et al. (2014) for this time period.

For the sake of brevity, we choose to include only four simulations; these nonetheless illustrate a key point regarding mathematical modeling: a known outcome (i.e., NEA extinction in 5,000 years) can be achieved by various mechanisms. We could have chosen to include many more simulations, but this would have merely provided more examples of the key point.

The four simulations correspond to quite different scenarios as explanations for NEA extinction, illustrating the flexibility and inclusivity of the model. This approach of beginning with a general and inclusive model that does not focus on one specific hypothesis allows investigators to broadly adapt mathematical (theoretical) models with archaeological evidence and data with impartiality.

We suggest that archaeologists might be able to assist mathematical modelers by providing an archaeological framework for a theoretical

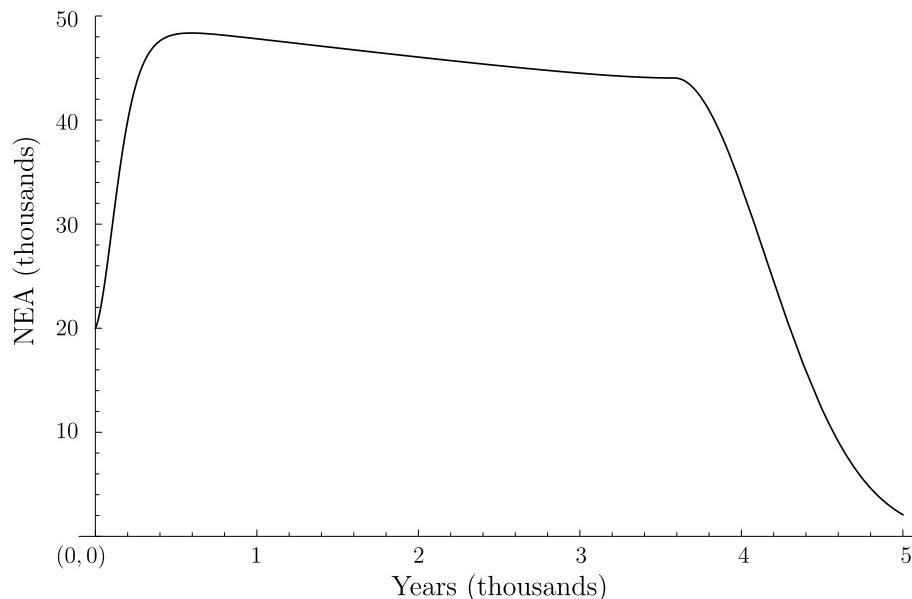


Fig. 7. Modeled NEA population dynamics if NEA birth rate and carrying capacity both decrease, and minimal death rate increases with the slight cooling of temperatures that occurred over the period 44,000 to 39,000 years ago.

mathematical model; specifically, by identifying key features of populations and cultures that must be included in a useful mathematical model, as well as by obtaining values of some of the parameters through field work, thus decreasing the number of possible scenarios. Some examples of parameter values that might be provided by field work include climatic influence over growth rate and carrying capacity of reindeer, maximal birth rates and minimal death rates of NEA and AMH, and maximal kill rates of reindeer by NEA and AMH.

We now describe the four simulations (Figs. 7–10) that provide illustrations of the two main hypotheses (climate change and competition) for NEA disappearance, including various forms of competition and/or interference within the context of competition (see Section 5.4).

Effect of temperature on NEA growth rate. In this simulation, NEA and AMH birth rates begin at the same value (4% per year). Ambient temperature in Europe declined slightly over the period under study (see Fig. 1), and we allowed NEA birth rate to decline with this temperature decrease, from 4% to 3%, and NEA carrying capacity to

decrease as well. The NEA minimal death rate also was allowed to increase with this temperature decrease. The result is that “growth rate = birth rate – death rate” becomes negative after 4,000 years and the modeled NEA population decreases to extinction over the next 1,000 years (see Fig. 7).

Based on both the archaeological evidence (See Section 2.2 and Fig. 2), as well as our simulation (see the Supplemental Mathematica Notebook for complete details), we conjecture that climatic adaptability of NEA was unlikely to be the singular cause for NEA extinction. According to our runs of this simulation, an approximate 20% detrimental influence of temperature on NEA's birth/death rates and carrying capacity are necessary for NEA extinction, which is not in agreement with the archaeological data indicating NEA were cold-adapted and quite capable of surviving the time period under consideration (See Section 2.2 and Fig. 2). Thus, we see no evidence (either archaeological or theoretical) that climate played a singular significant role in the disappearance of NEA.

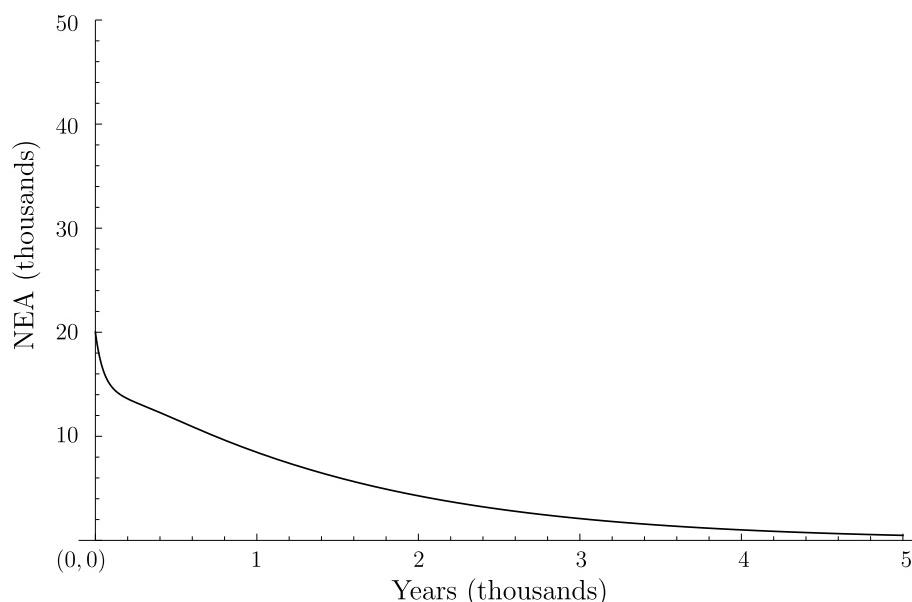


Fig. 8. Modeled NEA population dynamics if NEA minimal death rate is set at 4.1% per year (compared with 3% per year for AMH).

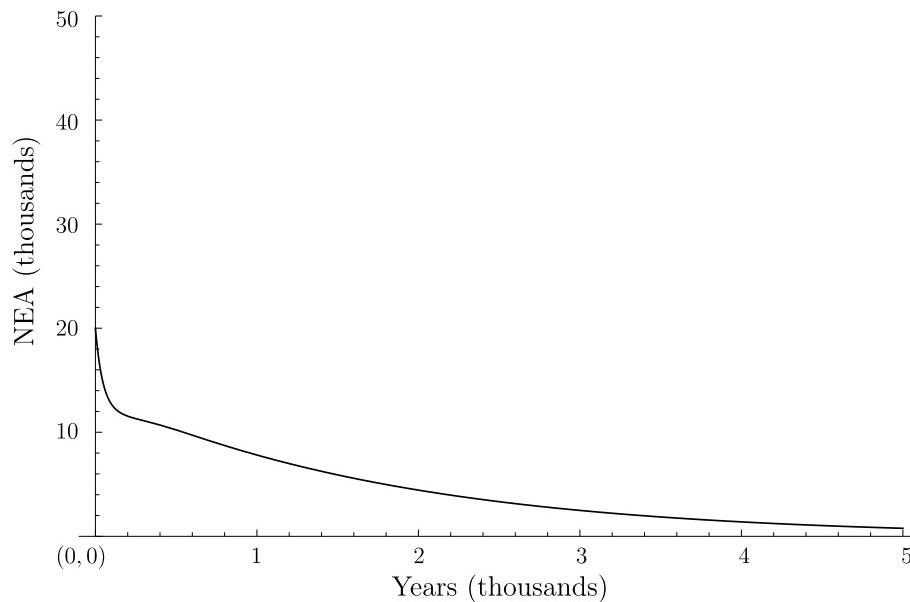


Fig. 9. Modeled NEA population dynamics if NEA death rate is higher than that of AMH ($d_1(t) > d_2(t)$ and $v_1 > v_2$ in Fig. 4).

In addition, this simulation indicates that our model can be used as a platform to continue to explore the climatic adaptability hypothesis for NEA extinction. It also demonstrates that the model could be used to investigate climatic influences for any two populations competing for a common resource.

Effect of higher minimal death rates in NEA. In this simulation, the minimal death rate for NEA is set at a higher level than for AMH (4.1% compared to 3%, $d_1 > d_2$ in Fig. 4). The NEA population size decreases regularly until extinction (see Fig. 8).

As pointed out above in our baseline case, a higher minimum death rate for NEA does not necessarily lead to NEA extinction. However, if the minimal death rate for NEA is sufficiently higher than AMH, then NEA could go extinct in 5,000 years as this simulation demonstrates. Our runs of this simulation suggest that the minimal death rate for NEA needs to be approximately 25% higher than AMH's minimal death rate (see the Supplemental Mathematica Notebook for complete details). We conjecture that this is too high according to the archaeological

evidence, which suggests only a slightly higher death rate for NEA (Pettitt, 2000), to be the sole viable explanation for NEA extinction.

This simulation indicates that our model can be used as a platform to continue to explore the corresponding hypothesis for NEA extinction. It also demonstrates that the model could be used to investigate the effect of different minimal death rates for any two populations competing for a common resource.

Effect of higher NEA death rate at any Resource level. In this simulation, the NEA death rate remains higher than that of AMH for any value of Resource availability ($v_1 > v_2$ in Fig. 4). NEA groups thus spend more time in initial hunting forays before they bag a reindeer, and the result is lower hunting success and extinction of NEA in 5,000 years (see Fig. 9).

Our runs of this simulation suggest that an approximate 6% advantage for AMH relative to this parameter is sufficient for NEA extinction in 5,000 years (see the Supplemental Mathematica Notebook for complete details), which is intriguing to consider. Indeed, we wonder

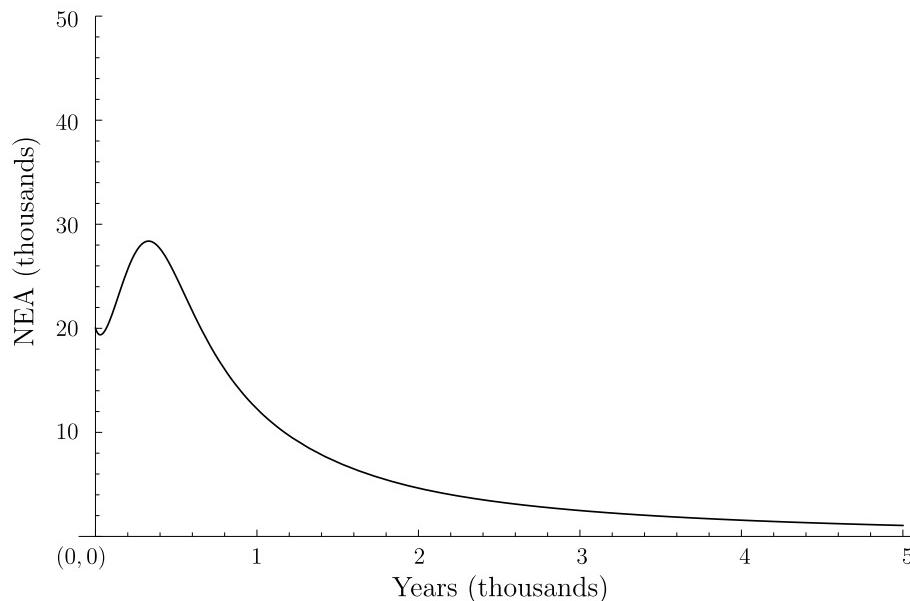


Fig. 10. Modeled NEA population dynamics if interference is more detrimental to NEA ($k_1 > k_2$).

whether there is archaeological evidence to suggest such an advantage—perhaps due to hunting strategies related to a cultural advantage. It is our hope that this observation may provide some guidance for archaeological findings and further exploration.

This simulation indicates that our model can be used as a platform to continue to explore the corresponding hypothesis for NEA extinction. It also demonstrates that the model could be used to investigate associated differences in death rates for any two populations competing for a common resource.

Effect of AMH interference on NEA. In this simulation, the populations AMH and NEA are allowed to interfere with each other. We consider the situation where the effect of interference is more detrimental to NEA. Thus, $k_1 > k_2$ in Equations (1) and (2) (see Fig. 10). See Section 5.4 for a discussion of various forms of interference that might influence the values for k_1 and k_2 .

Our runs of this simulation suggest that a competitive advantage for AMH relative to this parameter on the order of 1.6 ($k_1 \approx 1.6k_2$) is sufficient for NEA extinction in 5,000 years (see the Supplemental Mathematica Notebook for complete details), which is intriguing to consider. Indeed, we wonder whether there is archaeological evidence to suggest such an advantage—perhaps due to some subset of the modes of interference previously mentioned (see Section 2.3.2) and discussed in detail in Section 5.4. It is our hope that this observation may provide some guidance for archaeological findings and further exploration.

This simulation indicates that our model can be used as a platform to continue to explore the corresponding hypothesis for NEA extinction. It also demonstrates that the model could be used to investigate differences in interference for any two populations competing for a common resource.

Summary of simulations. As demonstrated with our four simulations, the model is not constructed to focus on a particular hypothesis regarding NEA extinction. Instead, the model is designed to be inclusive of a wide variety of hypotheses and associated archaeological evidence; therefore, providing investigators with a platform to examine various hypotheses (individually or in combination) with impartiality.

The four simulations were chosen for this publication because they all produced the accepted NEA extinction pattern: disappearance by 5,000 years after the arrival of AMH in Europe. Moreover, each of the simulations corresponds to either the climatic (Fig. 7) or the competition (Figs. 8–10) hypotheses. That the known outcome can be achieved by four quite different mechanisms (spanning the climatic and competition hypotheses) suggests that one cannot be confident in any particular hypothesis simply because it is fit by a simulation.

Criteria for parameter values that give a competitive advantage to AMH are described in Section 5.4. We recognize that our arbitrarily chosen initial number of NEA (20,000) influenced the parameter values that led to extinction in 5,000 years; but the values are not themselves important in the sense that given any reasonable initial population, one can choose values for the other parameters to obtain extinction of NEA in 5,000 years.

The four simulations illustrate that mathematical models and archaeological evidence can each contribute to an understanding of the population dynamics between NEA and AMH (see Section 3 for a broad discussion). We reiterate that we are not trying to demonstrate what caused NEA extinction; we are attempting instead to illustrate the usefulness to archaeologists and mathematical modelers of a clearly stated model. Our work suggests that if a model is sufficiently flexible and inclusive, it can be useful for the process of setting up hypotheses and trying likely scenarios, as well as identifying relevant parameters that are the most influential on the population dynamics. This provides archaeologists with some guidance as to which parameters are most important to estimate using archaeological evidence as suggested in the four simulations.

We point out that while we presented the four simulations individually, they are not necessarily mutually exclusive. If desired, an investigator could of course consider combinations of various scenarios;

for example, considering a small detrimental influence of climate on NEA's parameters and a small competitive advantage for AMH due to interference ($k_1 > k_2$), where each scenario by itself is not sufficient for NEA extinction, but taken together yield NEA extinction in 5,000 years. Because of the inclusive nature of our model, such combined hypotheses (there are too many to enumerate) are possible to explore—and exploration is encouraged.

It is our hope that our impartially constructed model will be an accessible resource for investigators who wish to examine any of the various hypotheses for NEA disappearance, as well as assist archaeologists with identifying relevant parameters that need estimating; thus, we propose this model as a way to contribute to an understanding of why NEA became extinct.

5.4. Modeling various forms of interference

Interference between NEA and AMH may occur in various forms, any of which could result in a competitive advantage for one of the populations. For example, a competitive advantage could be due to a difference in culture level or learning ability, a physiological difference, interbreeding, epidemics, or conflict. Here we discuss how an investigator can examine various scenarios using our model. The simulations presented in Section 5.3 provide illustrations corresponding to each of the forms of interference.

Culture level or learning ability. An investigator could examine the situation where one of the two human populations is culturally more advanced than the other (e.g., Gilpin et al., 2016; Horan et al., 2005), thus giving that one a competitive advantage with regard to resource usage and efficiency, or interference. Indeed, such a situation could be investigated using our model by examining simulations where, for example, AMH can be given a competitive advantage over NEA by setting some (or all) of the following parameters in Equations (1)–(3) so that:

$$r_2(t) > r_1(t) \quad (\text{higher maximal birth rate for AMH})$$

$$d_2(t) < d_1(t) \quad (\text{lower minimal death rate for AMH})$$

$$M_2(t) > M_1(t) \quad (\text{higher maximal carrying capacity for AMH})$$

$$a_2 < a_1 \quad (\text{AMH more efficient at resource usage in birth rate})$$

$$v_2 < v_1 \quad (\text{AMH more efficient at resource usage in death rate})$$

$$c_2 < c_1 \quad (\text{AMH more efficient at approaching its carrying capacity})$$

$$k_4 > k_3 \quad (\text{AMH have a higher maximal kill rate of Resource})$$

$$b_2 < b_1 \quad (\text{AMH more efficient at killing the Resource})$$

$$k_2 < k_1 \quad (\text{Interference is more detrimental to NEA})$$

Some possible scenarios that illustrate how cultural differences may affect NEA population size are shown in Figs. 8–10.

Physiological differences. An investigator could examine the situation where, for example, AMH has a physiological competitive advantage over NEA. Such a situation might be caused by a higher maximal birth rate, lower minimal death rate, more efficient resource usage, disease resistance, or another feature that may be modeled (similar to those mentioned due to culture level or learning ability) in ways that produce the results seen in Figs. 8–10.

Interbreeding. We have chosen not to explicitly include interbreeding in our model with the creation of a third (hybrid) population. However, we propose that any hybrid offspring is most likely to live with its mother—increasing the mother's population. This scenario could be investigated using the interference term in our model; for example, decreasing k_2 in Equation (2) for an AMH mother. This situation is illustrated in the simulation shown in Fig. 10 provided $k_2 < k_1$. An investigator could examine a non-equal effect of interbreeding by assuming different values for the interference coefficients k_1 and k_2 . For example, to investigate interference only in the form of interbreeding

that overwhelmingly favors AMH, assume $k_2 < 0$ and $k_1 \approx 0$.

Epidemics. An investigator could examine the situation where, for example, AMH passes a disease to NEA (Houldcroft and Underdown, 2016) by modeling such a transfer through the interference terms ($k_1 > k_2$) in Equations (1) and (2). This situation is illustrated in the simulation shown in Fig. 10.

An investigator could examine the situation where a population experiences a disease not necessarily being passed from another population. For example, we conjecture that a disease might affect the birth rate, death rate and ability to hunt. The effect could be modeled by adjusting the values of a population's parameters. For example, assuming NEA experiences a disease, an investigator could adjust $r_1(t)$, $d_1(t)$, $M_1(t)$, a_1 , v_1 , b_1 , c_1 and k_3 accordingly. This situation is illustrated in the simulation shown in Fig. 8.

Conflict. An investigator could examine the situation where AMH and NEA are warring populations through the interference terms in Equations (1) and (2). Assuming, for example, that AMH had a competitive advantage due to superior weaponry, tactics, etc., then one could take $k_1 > k_2$ in the simulations. This situation is illustrated in the simulation shown in Fig. 10.

5.5. Other hypotheses for NEA extinction

As previously mentioned, our model can accommodate both the climatic and competition hypotheses. In addition, our model is flexible enough to simulate many different situations in population dynamics; indeed, it invites investigators to develop new hypotheses. For example, our model can be used to explore the effects of random or contingent accidents on a small initial population size, as well as to investigate effects of spatial distributions of AMH, NEA and Resource populations. Other recent hypotheses for the replacement of NEA are AMH immigration and random species drift (Kolodny and Feldman, 2017).

NEA extinction as a statistical accident. An investigator could examine the situation where NEA extinction is a result of statistical variation because of small initial population size. By using the supplementary Mathematica Notebook, this can be explored by considering a small initial NEA population that results in the NEA population quickly approaching zero, and examining the stability of this situation numerically with respect to small variations in the parameters. We chose not to include this scenario as one of our simulations because NEA extinction as a statistical accident is unlikely to be the case since the initial NEA population size was large and stable prior to the arrival of AMH (Prüfer et al., 2014).

Incorporating spatial effects. The replacement process of NEA by AMH can be *self-perpetuating*. That is, an AMH population that has replaced a localized NEA population will be in position to invade the nearby region still occupied by NEA. This could be simulated by applying our model to a particular region, yielding population sizes for NEA, AMH and Resource at a particular value of time to be decided upon, and using these population sizes as the initial population sizes for the next region (e.g., Sørensen, 2011; Zubrow, 1989, 2000). Similar to some previous models (e.g., Faria, 2000; Flores, 1998; Gilpin et al., 2016), we chose not to explicitly include this process as one of our simulations.

Immigration and drift. Kolodny and Feldman (2017) developed a model that suggests a recurring immigration of AMH was sufficient to result in the replacement of NEA even if neither population had a selective advantage over the other. Similar to previous models (see Section 4), we chose not to incorporate a random drift process into our model—although we include an immigration term (see Section 5.2), which allows an investigator to consider the effect of different rates of recurring immigration of AMH with regard to the replacement of NEA.

5.6. Numerical analysis

Given a set of values for the parameters, a solution to our model is numerically constructed using a Runge-Kutta fourth-order method with

a variable time step that adapts itself to the rate of convergence of the numerical solution. Please see the Supplemental Mathematica Notebook for our code, and Mathematica's Documentation Center (Wolfram Research, 2012) for a detailed description of the numerical method associated with the command NDSolve that we employ in our code.

Because of the complexity of our model, we do not include a classical mathematical analysis (Murray, 2003) of Equations (1)–(3). We have nonetheless performed some numerical analysis regarding solutions to Equations (1)–(3). Specifically, a *sensitivity analysis* was performed for the four simulations (see Section 5.3) included in this paper. We observe that each of the four simulations is qualitatively stable (the solution's behavior remains) with respect to small perturbations of the chosen values for the parameters that produce a specific simulation. The specific values corresponding to the small perturbations are difficult to quantify because of the complexity of our model. An investigator interested in exploring the specific values may use the supplementary Mathematica Notebook, which provides an accessible platform.

As another example of sensitivity analysis and the qualitative stability of solutions, we have observed that coexistence of NEA and AMH is theoretically possible via the previously discussed baseline case, where we observe that each population approaches its carrying capacity. We numerically observe that this behavior (coexistence of NEA and AMH) continues to remain for sufficiently small perturbations of the chosen values for the interference coefficients (k_1 and k_2) and resource competition coefficients (k_3 and k_4). This result indicates that coexistence is a qualitatively stable phenomenon, and thus theoretically observable as a scenario. In other words, certain parameter values allow for the persistence of both NEA and AMH. The Supplemental Mathematica Notebook provides an accessible platform for an investigator interested in exploring coexistence and the specific values of the parameters that yield this behavior.

In addition, performing a sensitivity analysis can provide an investigator with broad insights with regard to identifying which parameters are the most influential in qualitatively affecting the population dynamics of NEA and AMH. For example, our simulations suggest that the interference coefficients k_1 and k_2 are more influential than the resource usage parameters a_1 , a_2 , c_1 , and c_2 . Such insights provide guidance as to which parameters are more important to estimate using archaeological evidence.

6. Summary and conclusions

Our model allows investigators to explore each of the two main categories (climatic adaptability of NEA or competition) regarding the disappearance of NEA. We do not singularly focus on identifying whether climate, competitive interactions, or any other ecological or cultural feature caused NEA extinction, and our model is designed to be inclusive of a wide variety of hypotheses and associated archaeological evidence. The inclusiveness of the model provides investigators with an accessible framework to examine with impartiality various hypotheses (individually or in combination) regarding climatic effects, differential resource use, differences in birth/death rates and carrying capacities, competition, interference, disease, interbreeding, and cultural distinctions that might have led to the extinction of NEA. Thus, we propose our model as a contribution to the understanding as to *why* NEA became extinct.

As an illustration of the inclusive nature and flexibility of our model, we provide four simulations of our model that achieve NEA extinction in 5,000 years after the arrival of AMH, consistent with the archaeological evidence. Each of the simulations is based on a different hypothesis for NEA extinction, illustrating that one cannot assign causality to a particular hypothesis simply because it produces a known outcome.

In addition, the simulations illustrate two key features of our model for examining hypotheses for NEA extinction. First, the simulations demonstrate how investigators may use our model to formulate

conjectures viewed within the context of existing archaeological evidence; second, the simulations demonstrate how our model may provide guidance for future archaeological studies.

Regarding the first key feature, some conclusions might be formulated. Specifically, based on runs of our simulations and the archaeological evidence, we conjecture it is likely that neither climate adaptability nor a higher minimal death rate for NEA were each solely responsible for NEA extinction (see Section 5.3).

Regarding the second key feature, we observe that (1) small advantages for AMH relative to resource usage, and (2) interference being slightly more detrimental to NEA could each be solely responsible for NEA extinction. As far as we are aware, no archaeological evidence addresses either hypothesis (1) or (2). While runs of our simulations suggest that either of the two hypotheses is a theoretically reasonable explanation for NEA extinction, without contextual archaeological evidence it is difficult to decide whether either actually caused NEA extinction. We hope these observations provide some guidance for further archaeological exploration (see Section 5.3).

We reiterate that although we have framed our model in terms of the two populations NEA and AMH, the model is general in the sense that it could apply to a wide range of any two populations competing for a common resource. Specifically, our model provides investigators—both mathematical modelers and archaeologists—with an accessible platform for examining hypotheses for the extinction of many types of populations, as well as for examining the likelihood of future extinction of a population that completes with another population for a common resource. Moreover, our model is a modification of the classical Lotka-Volterra model by including the common resource as another variable, a dependence of important population parameters on resource, as well as by including an immigration term—allowing an investigator to treat one of the populations as invasive.

In summary, we propose a mathematical model that can be used by any investigator wanting to explore the basis for NEA extinction 39,000 years ago. It is flexible and inclusive enough to examine a large number of possible hypotheses for the disappearance of NEA—not focusing on one specific hypothesis. We propose our model in the spirit of applying archaeological findings to mathematical modeling, and conversely applying the concepts of population dynamics and ecology to archaeological investigations. We suggest that it will give anthropologists an ecological basis for hypothesis testing and estimating values of relevant parameters within a mathematical model (e.g., deciding what features of human population dynamics to search for while excavating). In addition, if modelers such as population ecologists have access to human population information (i.e., specific birth rates, death rates, or hunting efficiencies), they might be able to run simulations that more accurately reflect real populations. We propose this modeling approach in the hopes that it may be useful in many types of population dynamics investigations, including that of NEA disappearance.

Conflicts of interest

The authors confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2018.09.012>.

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